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VITAMIN B REQUIREMENTS OF DROSOPHILA MELANOGASTER[1]

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Drosophila melanogaster larvae, grown under aseptic conditions on an agar medium containing amino acids, carbohydrate, salts and certain vitamins, require in addition, for normal growth and complete development to the adult state, three distinct fractions obtainable from yeast. The available information on the properties of these yeast fractions may be summarized as follows:[2]

Fraction I—water and alcohol insoluble; residue from yeast autolyzate.[3,4]

Fraction II—water soluble; alcohol extract of dried brewer's yeast.

Fraction III—water soluble; precipitated by barium hydroxide and alcohol from yeast extract.

The nutritional effects of various combinations of these fractions for Drosophila larvae are:

Fractions I, II or III separately—no growth.

Fractions I + II, or I + III—puparium formation, no subsequent development.

Fractions II + III—slow growth but otherwise normal development.

Fractions I + II + III—completely normal growth and development.

It has been shown that even with all three added yeast fractions, riboflavin was a limiting essential factor. It was also shown that nicotinic acid was one of the essential substances contained in fraction II. The present paper deals with the nature of the other essential substances present in this yeast fraction. It has been found that a combination of nicotinic acid, vitamin B_1, vitamin B_6 and pantothenic acid[5] completely replaces fraction II in the nutrition of Drosophila larvae.

The methods of obtaining and culturing sterile Drosophila larvae followed in this investigation have been previously described.[2,6] As before, the vermilion brown mutant of *Drosophila melanogaster* was used.

An attempt was made to remove all the components of fraction II from dried brewer's yeast by grinding it with silica powder and extracting very thoroughly with hot alcohol. Feeding tests of the exhausted residue indicated that nicotinic acid is completely removed. The results in table 1 show that the addition of vitamins B_1, B_2 and B_6 and of cholesterol did not restore the effectiveness of this extracted yeast residue. The addition of nicotinic acid alone did so partially. However, with nicotinic acid alone, some animals still failed to develop after puparium formation, indicating that another component of fraction II had been partially extracted from the dried yeast, and was a limiting factor. The evidence indicates that this was vitamin B_1 since the addition of nicotinic acid with B_1 led to slightly faster growth than with nicotinic acid alone, and to

TABLE 1

EXTRACTION OF FRACTION II FROM DRY YEAST

Medium contained per 10 cc.: 0.1 g. alcohol extracted dry yeast; 0.1 g. sucrose; and 0.15 g. agar

SUPPLEMENTS ADDED	PUPARIUM FORMATION NUMBERS	PUPARIUM FORMATION DAYS	ADULT FLIES NUMBERS	ADULT FLIES DAYS	COMMENTS
None	..	...	..	...	Larvae died in 3 to 5 days
B_1, B_2, B_6 and cholesterol	..	...	..	...	Larvae died in 3 to 5 days
Nicotinic acid	43	6–8	34	10–13	9 failed to develop after puparium formation
Nicotinic acid, B_1, B_2, B_6 and cholesterol	45	5–8	42	10–11	Normal development in all cases
Nicotinic acid and B_1	50	5–7	48	10–11	Normal development in all cases

Amounts of supplements per 10 cc. medium:
B_1, 2 γ; B_2, 5 γ; B_6, 10 γ; nicotinic acid, 10 γ; cholesterol, 0.1 mg.

completely normal development. Since it is known[2] that nicotinic acid with vitamin B_1 cannot replace fraction II in media containing fractions I and III, it must be assumed that there are still other components of fraction II which cannot be removed completely enough to be limiting by this procedure of extracting dried yeast with alcohol.

Further investigations were therefore undertaken using a basal medium containing amino acids, carbohydrate, yeast ash, nicotinic acid, vitamins B_1 and B_2, with cholesterol and yeast fractions I and III. Since the properties of the known components of the vitamin B complex suggest that they might be responsible for the activity of fraction II for Drosophila larvae, the possibility of replacing this fraction by other components of the B group was investigated.

The results given in table 2 show that although no growth took place on the unsupplemented medium, the addition of vitamin B_6 partially

restored the effectiveness. No effect of β-alanine and choline could be demonstrated. The optimum effect of B_6 was reached with a concentration of 5 γ per 10 cc. However, nearly half of the animals failed to grow normally and those that formed puparia did not do so until 9 days after egg laying (normal time, 5 days). All animals which formed puparia developed normally. This result indicated that some component of fraction II other than vitamins B_1, B_2, B_6, and nicotinic acid was still present, but in limiting amounts, in the fraction I used in these experiments.[3] (The fraction I used in the previous experiments[2] apparently was freer of this contaminating II component—later shown to be pantothenic acid—since it permitted no development after puparium formation under comparable conditions.) This was proved by the failure of added vitamin

TABLE 2

PARTIAL REPLACEMENT OF FRACTION II WITH VITAMIN B_6-HCl

Medium contained per 10 cc.: hydrolyzed casein, 0.2 g.; l-tryptophane, 5 mg.; sucrose, 50 mg.; yeast ash, 14 mg.; B_1, 2 γ; B_2, 5 γ; nicotinic acid, 10 γ; cholesterol, 0.1 mg.; agar, 0.15 g.; yeast fraction III, equivalent to 0.3 g. yeast extract; yeast fraction I, 0.1 g. (50 eggs used for each series).

SUPPLEMENTS ADDED	PUPARIUM FORMATION NUMBERS	PUPARIUM FORMATION DAYS	ADULT FLIES NUMBERS	ADULT FLIES DAYS	COMMENTS
None	..	...	..	...	Larvae died in 8–10 days
β-Alanine, choline, B_6	27	9–10	24	14–15	Normal development
β-Alanine, choline	..	...	..	...	Larvae died in 8–10 days
B_6-HCl, 5 γ	25	8–10	23	13–14	Normal development
" 10 γ	24	8–10	21	13–14	Normal development
" 20 γ	23	8–10	18	13–14	Normal development
" 40 γ	30	8–10	24	13–14	Normal development
" 20 γ (yeast fraction I omitted)	20	13–15	..	...	Died after puparium formation

Amounts of supplements per 10 cc. medium unless otherwise specified: β-Alanine, 1 mg.; choline-HCl, 10 γ; B_6-HCl, 20 γ.

B_6 alone to permit any development after puparium formation on the same basal medium from which fraction I had been omitted. A combination of yeast fractions II and III gives slow growth but normal development.[2]

Fraction I was therefore reëxtracted with water several times by autoclaving in water suspension and centrifuging, so as to remove the contaminating II component as completely as possible. In the presence of fraction III and vitamin B_6 this purified fraction I permitted about the same percentage of puparium formation as was obtained using the unextracted fraction I, but only a very few animals developed normally to the adult state. This showed that the impurity had been largely removed. Table 3 gives the results of additional supplements of other growth factors; pantothenic acid,[5] inositol, choline, β-alanine and pimelic acid. The

combination of these factors permitted completely normal growth, with no cases of abnormal development. It was found that pantothenic acid alone was responsible for this restoration. (β-Alanine was ineffective.) Table 3 also shows that with an increase in pantothenic acid concentration, both the number of animals forming puparia and the number of these which developed normally after puparium formation increased until at a concentration of 10 γ calcium pantothenate per 10 cc., puparium formation took place almost as early as on a medium of living yeast (normal food) and development was completely normal. Furthermore, in contrast

TABLE 3

PANTOTHENIC ACID REQUIREMENTS

Medium: same as in table 2, except that thoroughly extracted yeast fraction I was used, 0.1 g. per 10 cc.; and vitamin B_6-HCl was added, 10 γ per 10 cc. (50 eggs used in each series).

SUPPLEMENTS ADDED	PUPARIUM NUMBERS	PUPARIUM FORMATION DAYS	ADULT FLIES NUMBERS	ADULT FLIES DAYS	CASES OF ABNORMAL DEVELOPMENT AFTER PUPARIUM FORMATION
None	21	9–11	2	13	19
Calcium pantothenate, inositol, choline, β-alanine, and pimelic acid	48	7–8	45	11–13	None
Calcium pantothenate	45	7–8	43	11–12	None
Calcium pantothenate (yeast fraction I omitted)	10	18–20	9	21–23	None
None	31	9–10	6	14–15	25
Calcium pantothenate, 1 γ	43	8–9	27	12–13	16
Calcium pantothenate, 5 γ	29	7–8	29	11–12	None
Calcium pantothenate, 10 γ	41	6–8	41	10–11	None
Calcium pantothenate, 25 γ	43	7–8	43	11–12	None
Calcium pantothenate, 50 γ	42	6–8	41	10–11	None

Amounts of supplements per 10 cc. medium unless otherwise specified:
Calcium pantothenate, 50 γ; inositol, 10 mg.; choline-HCl, 10 γ; β-alanine, 1 mg.; pimelic acid, 0.1 mg.

to the inability of the larvae to grow normally and develop on the medium without fraction I and supplemented only with B_1, B_2, B_6, nicotinic acid and fraction III (see table 2), the same medium with the addition of pantothenic acid permitted complete but quite slow development of an appreciable number of animals. This is comparable to the growth on a combination of yeast fractions II and III.[2]

These results agree with the recent findings of SubbaRow and Trager[7] that mosquito larvae require vitamins B_1, B_2, B_6 and pantothenic acid, and probably nicotinic amide, as well as other unknown factors. The fact that for mosquito larvae these vitamins must be added to a medium

already containing killed yeast, indicates that these insect larvae have considerably higher requirements of these factors than Drosophila, since for the latter a concentration of unsupplemented dry yeast of 30 to 50 mg. per 10 cc. is adequate for growth.[6] The requirement of about 10 γ pantothenic acid per 10 cc. by Drosophila larvae is very much lower than the needs of mosquito larvae of 400 γ per 10 cc.[7] It seems possible also that the "B_x" factor described by Fröbrich[8] and by Offhaus[9] as essential for *Tribolium confusum* (flour beetle) may be related to pantothenic acid.

The statement of SubbaRow and Trager[7] that "insects require the same growth factors of the vitamin B complex as do vertebrates" is supported by the findings with Drosophila. Since the five B vitamins: B_1, B_2, B_6, nicotinic acid and pantothenic acid[10,11] seem to satisfy the requirements of Drosophila,[12] one might even go further and say that they are the only components of the vertebrate vitamin B complex which must be supplied to Drosophila larvae. The apparently more exacting requirements of mosquito larvae indicates that this may not be true for other insects. (See Trager[13] for a comprehensive review of invertebrate nutrition.) Both Drosophila and mosquito larvae require additional factors of as yet unknown nature. Investigation of the yeast fractions I and III needed by Drosophila larvae is being continued.

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[2] Tatum, E. L., *Proc. Nat. Acad. Sci.*, **25**, 490 (1939).

[3] In the previous report[2] it was concluded that fraction I is present in filtered yeast autolyzate and was removed from Difco yeast extract (an autolyzate) by adsorption on the filter mass used. Further investigation has shown that fraction I is actually insoluble in water, but is present in centrifuged or filtered yeast autolyzate in a colloidal suspension, and is therefore removed by the filter mass. The insoluble I used in these experiments was obtained from yeast autolyzate without using filter mass and therefore could not as easily be washed free of last traces of soluble constituents. The author is indebted to the Difco Laboratories, Detroit, Michigan, for their coöperation in preparing this and other yeast fractions used in establishing these points.

[4] The insoluble nature of fraction I suggests its similarity to the insoluble factor "U" required by Tribolium.[8,9]

[5] Williams, R. J., and Major, R. T., *Science*, **91**, 246 (1940). A sample of synthetic dextro-rotatory calcium-pantothenate was very kindly supplied by the Research Laboratory of Merck and Company, Inc., Rahway, N. J.

[6] Tatum, E. L., and Beadle, G. W., *Biol. Bull.*, **77**, 415 (1939).

[7] SubbaRow, Y., and Trager, W., *Jour. Gen. Physiol.*, **23**, 561 (1940).

[8] Fröbrich, G., *Z. vergleich. Physiol.*, **27**, 335 (1939).

[9] Offhaus, K., *Ibid.*, **27**, 384 (1939).

[10] Wooley, D. W., Waisman, H. A., and Elvehjem, C. A., *Jour. Amer. Chem. Soc.*, **61**, 977 (1939).

[11] Jukes, T. H., *Ibid.*, **61**, 975 (1939).

[12] It seems improbable that yeast fractions I and III or the acid hydrolyzed casein used in these experiments should contain any other vitamins ordinarily included in the vertebrate B group.

[13] Trager, W., *Physiol. Rev.*, **21**, 1 (1941).

THE ELECTRIC STIMULATION OF THE CONCENTRATING (ADRENERGIC) AND THE DISPERSING (CHOLINERGIC) NERVE-FIBRES OF THE MELANOPHORES IN THE CATFISH

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1. Introduction.—The integumentary melanophores in the lower vertebrates were supposed for a long time to be under the exclusive control of a single set of nerve-fibres. When in many of these animals nerves containing melanophoral fibres were stimulated electrically, the appropriate areas of skin blanched through the concentration of pigment in their melanophores. This phase of the color cells was therefore regarded as the active one. When these nerves were cut, the resulting dark areas were believed to be due to the local paralysis of the part of the melanophore system thus denervated and the state of dispersed pigment was interpreted as that of rest for the color cells. This view, which was first advanced by Brücke (1852) in his classical monograph on the color changes of the African chameleon, was accepted for fishes by both Pouchet (1876) and von Frisch (1910, 1912) and has been adhered to even in comparatively recent times for reptiles as well as for fishes by Sand (1935) and by Wykes (1938).

As opposed to the idea that melanophores are singly innervated is the hypothesis, first suggested by Bert (1875), that these color cells may have a double innervation one set of fibres being concerned with the concentration of the melanophore pigment and the other with its dispersion. In recent years this view has been revived at least for certain animals (Parker, 1932) and more or less evidence has been accumulated in its favor. Spaeth and Barbour (1917), Giersberg (1930) and Smith (1931) have all published results on the reactions of fish melanophores to drugs that favored the idea of double innervation. Mills (1932), who studied the melanophores on the edges of caudal bands in killifishes, showed that these edges were not constant when the fish changed from dark to pale or the reverse, a condition difficult to explain without the assumption of double innervation. Parker (1934*a*) pointed out that when a dark caudal band that had subsequently blanched was recut immediately distal to the region where the initiating cut had been made, the band again became dark. This reactivation of the band demonstrated that the portion of the melanophore system in the band had not been paralyzed by the first cut but was merely quiescent and further that the nerves cut must be assumed to contain dispersing fibres. Abramowitz (1935) also demonstrated that when the caudal nerves in killifishes and in catfishes were in process of regeneration, melanophores

could be found on the front edge of the regeneration area that could expand but not contract or the reverse, again a condition difficult to elucidate without assuming double innervation. The presence of dispersing fibres in these caudal nerves was also indicated by antidromic reactions in the dark caudal bands of the killifish (Parker, 1937).

Thus more or less evidence was marshaled in favor of the hypothesis of double innervation at least for certain fishes, but a serious obstacle to the acceptance of this view lay in what was known concerning the electric stimulation of chromatophoral nerves in these animals. If two sets of chromatic nerve-fibres are present in caudal nerves, it ought to be possible to activate these sets separately by electric means. Although concentrating nerve-fibres have long been known to respond to this form of stimulation, dispersing fibres have never thus been shown to be present. Here then is a serious objection to the acceptance of the view that dispersing fibres really exist and that double innervation therefore actually occurs. It must be admitted, however, that the investigation of this question has been far from adequate. With recent improvements in electric appliances it seemed desirable to give this problem renewed study. The outcome of this reinvestigation is the subject of the present paper.

2. Material and Methods.—The work herein described was done on the fresh-water catfish, *Ameiurus nebulosus*, and specimens of this fish of medium size, about 15 to 18 cm. in length, were used. These fishes, as has long been known, have well-marked color phases pale and dark. In the pale condition the fish is a translucent greenish yellow and the pigment in each large dermal melanophore is concentrated into a ball some 45 microns in diameter. In the dark condition this pigment spreads throughout the branched processes of the melanophore and partly covers an area about 145 microns across. The change in the tint of the catfish from one extreme to the other is a relatively slow one and requires for its completion a day or more. In experimentation we found it convenient to use fishes of intermediate tint so that a color change in either direction could be easily detected.

Living catfishes when prepared for tests were wrapped except for their tails in wet cloth and bound down sidewise by a cord run through metal hooks on the top of an inclined wooden bench. Each fish was placed head downward on the slope of the bench. Through an opening in the enveloping cloth next the mouth of the fish a water-tube was introduced into the pharynx whereby an ample supply of fresh water could be passed over the fish's gills. Catfish thus held down remained quiescent for hours and on being released showed no signs of having suffered in any respect. The uncovered tail of the fish, which was spread out on the upper part of the inclined bench, was held firmly in place by means of half-a-dozen glass pushpins which were pressed through the edges of the tail and into the

wooden top of the bench. Thus the fifteen or more rays in the tail of the fish were exposed in such a way that platinum electrodes could be applied to any one of them and kept there with certainty and security for any desired length of time.

The electrodes were placed on the surface of the skin at the base of the tail, parallel to the ray which was to be stimulated. The interelectrodal distance was 8 mm. The cathode was usually peripheral. Direct current pulses from a multivibrator circuit were used as stimuli. The amplitude, duration and frequency of the shocks could be varied independently. No precautions were taken to render the electrodes impolarizable. The pulses delivered to the nerves were therefore of initial maximal amplitude, with a progressive decline determined by the counter e. m. f. of polarization. The voltages measured apply to the beginning of the pulses.

The catfishes upon which our experiments were made were kept in water whose temperature ranged from about 18° to 20°C.

3. Results.—The electric stimulation of the nerves contained in the caudal rays of *Ameiurus* has already been attempted. To blanch a whole dark killifish or a band in its tail by applying the electrodes from a Harvard inductorium to the region of the medulla oblongata or to the root of a caudal ray is so readily accomplished that it seemed only reasonable to look for similar results in the catfish. As a matter of fact, however, the first attempts in this direction yielded only negative results (Parker, 1934*b*). Abramowitz (1936) recorded a blanching of the catfish to electric stimulation of the medulla oblongata and of the anterior end of the spinal cord, and Osborn (1938) without stating where or how the stimulus was applied declared that electric excitation blanches catfishes. Wykes (1938) on the other hand reported on the subject with some fulness. She varied the strength and frequency of the electric stimulus used. With a discharge voltage that was barely perceptible on her tongue she used frequencies in current alternations of from two to fifty per second. No melanophore responses were noted when the electrodes were placed in the vertebral canal and the frequency was below ten per second, but at that rate the innervated parts of a dark fish blanched in five minutes and at fifty alternations per second the same response was to be seen in two minutes. According to these observations the concentrating nerve-fibres in the catfish appear to have been stimulated by weak condenser discharges whose frequencies were fifty or ten per second but not by those of the lower frequencies of four and two. At none of the frequencies tested was there evidence of the activation of dispersing nerve-fibres. The records of these several authors appear to be the only ones thus far reported on the electric stimulation of the chromatophoral nerves in catfishes and though they show, as already stated, evidence for the excitation of concentrating fibres they indicate

nothing from the electric standpoint that can be construed in favor of the stimulation of dispersing fibres.

Blanching responses were readily seen in the present observations after stimulation for 5 to 20 minutes at frequencies of 15 to 25 per second with pulses lasting from 4 to 8 msec. Approximately 8 volts were required for these reactions. In one experiment two cuts were made in the tail of a pale fish. Such cuts result in the appearance of a dark band within 5 to 15 minutes (Parker, 1934*b*). One of the cut rays was stimulated for 15 minutes, while the other was used as a control. While the unstimulated region developed a characteristic dark band within this period, the stimulated one became only slightly less pale than the rest of the tail.

These observations confirm the earlier work on blanching responses. Darkening effects were, on the other hand, regularly elicited when stimulation was carried out with slow frequencies (1 to 2 per second) and with long pulses (0.3 to 0.5 second). With such stimuli applied for 5 to 10 minutes an intensity of 4 volts had no results, either blanching or darkening; 6 volts resulted in a slight darkening; and 8 volts caused marked dark reactions. Effective stimuli of this kind though applied to only one caudal ray specifically commonly induced darkening in the two immediately adjacent rays probably by spread of the electric current. The large melanophores in the dark bands excited electrically covered areas which averaged about 120 microns in diameter.

The dark bands extended in the tail from the point where the cathode was applied to the periphery. When the anode was placed centrally the interelectrodal region did not darken.

In some pale fishes a dark band was produced by electrical stimulation for 10 minutes. A cut was then made in another region of the tail, which resulted in the appearance of an additional dark band. These two dark bands were then watched to ascertain the length of time for their disappearance. In all instances the bands excited electrically disappeared much sooner (in one or two days) than those excited by the cut (about ten days).

4. *Discussion.*—An important issue for the interpretation of the observations herein reported is whether the dark bands elicited by applications of relatively long direct current pulses were due to stimulation of underlying dispersing nerves or whether they were caused by injury or damage to concentrating fibres. Three arguments support the first of these alternatives. First, if the currents delivered had damaged the neighboring nerve elements, it is unlikely that this damage should have been limited to the region of the cathode, with the exclusion of the anode. Yet the dark bands appeared only distal to the cathode.

With weak voltages or brief periods of stimulation the bands which developed were not as dark as those resulting from stronger stimulation. If

darkening were the result of an irreversible nerve lesion, a uniform reaction would be expected in all instances.

Finally, more direct evidence against the view that the dark responses could be due to irreversible damage of nerve-fibres is furnished by the comparison of the bands caused by electric currents with those produced by cuts. Since the former disappeared more promptly than the latter, it is clear that the mechanism of production is different in the two cases.

It is well known that electric stimuli of certain characteristics may selectively activate certain nerve-fibres in a mixed group. It is also well known that changes in the frequency of stimulation may emphasize one out of several possible responses. It is likely from the present and previous observations that while brief and rapid shocks predominantly activate the concentrating fibres in the tail of the catfish, slow and long pulses elicit a preponderant dispersing reaction.

Previous observations (Parker, 1934*a*) led to the conclusion that the dark bands caused by cuts were due to a long-lasting, injury discharge of dispersing nerve-fibres, not to the paralysis of concentrating nerves. The present study supports this conclusion, since it indicates that there are dispersing fibres which may be stimulated electrically, and indicates further that the effects of such stimulation are relatively transient when compared with the effects of a cut. A long-lasting injury discharge is in contrast with the usual brief discharges encountered in mammalian nerves under similar circumstances. This contrast might disappear if the conditions which modify this discharge were better known. Thus, no systematic study is available on the influence of temperature upon injury discharge and on possible differences in fibres of different diameters and conduction velocities.

It is interesting to compare the neuro-effector systems under discussion with a nerve-smooth-muscle preparation. The melanophores require very prolonged stimulation before completion of either a concentrating or a dispersing response. Each nerve impulse must produce, however, a slight effect, for the response is not sudden, but gradual. Even in slow smooth-muscles, on the other hand, relatively few nerve volleys are sufficient to produce maximal effects. With two sets of nerve-fibres controlling opposite responses of the melanophores there is no criterion for defining a resting condition. Both concentration and dispersion are responses to specific stimuli. A similar view applies to certain smooth-muscle systems with double nerve supply (Rosenblueth and Cannon, 1934).

The evidence presented in this paper confirms the view that the melanophores in the catfish possess a double innervation, one set of nerve-fibres inducing a concentration of pigment, the other a dispersion. Judging from the reactions of other bony fishes (the killifish and the squirrel fish) this state may prove to be generally true for teleosts. It is not impossible

that this type of innervation occurs in the chameleons though it is absent quite clearly from other lizards such as Anolis (Kleinholz, 1938) and Phrynosoma (Parker, 1938). So far as the catfish is concerned evidence has already been advanced to show that the dispersing fibres are cholinergic and the concentrating fibres adrenergic in character (Chang, Hsieh, and Lu, 1939; Parker, 1940).

5. Summary.—1. Electric stimulation of the melanophore nerves in the tail of the catfish (*Ameiurus nebulosus*) over periods of 5 to 20 minutes, at frequencies of 15 to 25 per second, with pulses lasting from 4 to 8 msec., and at approximately 8 volts resulted in a blanching of the innervated region. This confirms earlier work. The nerve-fibers involved are probably adrenergic.

2. Electric stimulation of the same melanophore nerves over periods of 5 to 10 minutes, at frequencies of 1 to 2 per second, with long pulses, 0.3 to 0.5 second, at 6 to 8 volts resulted in a darkening of the innervated region. At 4 volts there was neither blanching nor darkening. The fibres concerned are probably cholinergic.

3. These results confirm the view that the melanophores in *Ameiurus* have a double innervation, a condition which probably also occurs in other teleosts and perhaps in the chameleon.

Abramowitz, A. A., "Regeneration of Chromatophore Nerves," *Proc. Nat. Acad. Sci.*, **21**, 137–141 (1935).

Abramowitz, A. A., "Physiology of the Melanophore System in the Catfish, *Ameiurus*," *Biol. Bull.*, **71**, 259–281 (1936).

Bert, P., "Sur le mécanisme et les causes des changements de coleur chez le caméléon," *C. R. Acad. Sci. Paris*, **81**, 938–941 (1875).

Brücke, E., "Untersuchungen über den Farbenwechsel des afrikanischen Chamäleons," *Denkschr. Akad. Wiss. Wien, math.-nat. Cl.*, **4**, 179–210 (1852).

Chang, H. C., Hsieh, W., and Lu, Y. M., "Light-Pituitary Reflex and the Adrenergic-Cholinergic Sympathetic Nerve in a Teleost," *Proc. Soc. Exp. Biol. Med.*, **40**, 455–456 (1939).

Von Frisch, K., "Ueber die Beziehungen der Pigmentzellen in der Fischhaut zum sympathischen Nervensystem," *Festschr. R. Hertwig*, **3**, 15–28 (1910).

Von Frisch, K., "Ueber farbige Anpassung bei Fischen," *Zool. Jahrb. Abt. allg. Zool. Physiol.* **32**, 171–230 (1912).

Giersberg, H., "Der Farbwechsel der Fische," *Zeit. vergl. Physiol.*, **13**, 258–279 (1930).

Kleinholz, L. H., "Studies in Reptilian Colour Changes. II. The Pituitary and Adrenal Glands in the Regulation of the Melanophores of *Anolis carolinensis*," *Jour. Exp. Biol.*, **15**, 474–491 (1938).

Mills, S. M., "The Double Innervation of Fish Melanophores," *Jour. Exp. Zool.*, **64**, 231–244 (1932).

Osborn, C. M., "The Role of the Melanophore-Dispersing Principle of the Pituitary in the Color Changes of the Catfish, *Ibid.*, **79**, 309–330 (1938).

Parker, G. H., *Humoral Agents in Nervous Activity with Special Reference to Chromatophores*, Cambridge, England, 79 pp. (1932).

Parker, G. H., "The Prolonged Activity of Momentarily Stimulated Nerves," *Proc. Nat. Acad. Sci.*, **20**, 306–310 (1934*a*).

Parker, G. H., "Color Changes of the Catfish *Ameiurus* in Relation to Neurohumors," *Jour. Exp. Zool.*, **69**, 199–223 (1934*b*).

Parker, G. H., "Do Melanophore Nerves Show Antidromic Responses?" *Jour. Gen. Physiol.*, **20**, 851–858 (1937).

Parker, G. H., "The Colour Changes in Lizards, Particularly in Phrynosoma," *Jour. Exp. Biol.*, **15**, 48–73 (1938).

Parker, G. H., "On the Neurohumors of the Color Changes in Catfishes and on Fats and Oils as Protective Agents for Such Substances," *Proc. Amer. Philos. Soc.*, **83**, 379–409 (1940).

Pouchet, G., "Des changements de coloration sous l'influence des nerfs," *Jour. Anat. Physiol.*, **12**, 1–90, 113–165 (1876).

Rosenblueth, A., and Cannon, W. B., "Direct Stimulation of Denervated Autonomic Effectors," *Amer. Jour. Physiol.*, **108**, 384–396 (1934).

Sand, A., "The Comparative Physiology of Colour Response in Reptiles and Fishes," *Biol. Rev.*, **10**, 361–382 (1935).

Smith, D. C., "The Action of Certain Autonomic Drugs upon the Pigmentary Responses of Fundulus," *Jour. Exp. Zool.*, **58**, 423–453 (1931).

Spaeth, R. A., and Barbour, H. G., "The Action of Epinephrin and Ergotoxin upon Single Physiologically Isolated Cells," *Jour. Exp. Pharm. Therap.*, **9**, 431–440 (1917).

Wykes, U., "The Control of Photo-Pigmentary Responses in Eyeless Catfish," *Jour. Exp. Biol.*, **15**, 363–370 (1938).

X-RAY INDUCED CHROMOSOME REARRANGEMENTS IN THE FEMALES OF SCIARA

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Metz and Boche[1] (1939) carried out a series of experiments "in order to get definite evidence regarding induced chromosome rearrangements" in the fungus gnat, *Sciara*. Since Dr. Helen Smith-Stocking[2] had previously been able to induce only a small number of mutations in *Sciara* with the use of x-rays and radium, and since Muller[3] and others had found that in *Drosophila* there seems to be a correlation between induction of gross chromosome rearrangements and induction of mutations, Metz and Boche expected a low frequency of induced rearrangements in *Sciara*. They found, however, that after subjecting adult males to 5000 r units an appreciable number of gross rearrangements could be induced. Approximately 27% of the larvae examined showed these aberrations. Adult females were similarly treated, but in these no gross changes were observed. As pointed out by the authors, this difference between chromosome sensitivity in males and females seemed to be at variance with the generally accepted views concerning conditions in *Drosophila*. In the latter, for example, Oliver[4] (1932) was able with x-rays to induce mutations

and chromosome aberrations in females as well as in males, although he found that "displacements" were less frequent in the former, in proportion to gene mutations. Indications of a sex difference in sensitivity in *Drosophila*, however, have been found by Shapiro and Volkova[5] (1938), who report a greater frequency of induced mutations in treating males than females. Still more recently Glass[6] (1940) has been able to demonstrate that there is a decided difference in the number of gross rearrangements of chromosomes induced by x-rays in male and female germ cells of *Drosophila*. By use of the salivary gland smear technique he found no translocations after treatment of females and a much smaller number of inversions than he found after similarly treating sperm.

Metz and Bozeman[7] (1940) have suggested that lack of chromosome movement during the mid-prophase may account for the "resistance" to irradiation of the chromosomes of oöcytes in *Sciara*. Dr. Anna R. Whiting[8] (1940) has found that prophase chromosomes in oöcytes of *Habrobracon* are much less sensitive to irradiation than are the chromosomes at metaphase. This may be correlated with the findings of Patterson,[9] who reports that in *Drosophila* there seems to be an increase in frequency of rearrangements in old, as compared with younger, eggs. Sonnenblick[10] (1940) reports that in *Drosophila* "especially susceptible to the radiations are the most mature oöcytes." This conclusion was based on a comparative study of the mortality of zygotes from oöcytes and mature sperm which had been treated with x-rays.

If lack of movement is a factor in chromosome rearrangement, as suggested by Metz and Bozeman (loc. cit.), then it might be expected that rearrangements could be induced in oöcytes at a later stage than those previously involved. The present investigation was designed to explore this possibility. The study is in only its initial stages, but it seems advisable to present the data thus far obtained.

In *Sciara* all eggs develop synchronously, a condition not existing in *Drosophila*. This makes possible the irradiation of a large number of oöcytes at any given stage in the meiotic process.

Before an intelligent approach to the problem could be made, it was necessary first to ascertain at what stage in the meiotic process the chromosomes were to be found during successive hours after emergence. Metz and Bozeman (loc. cit.) had previously described the condition of the chromosomes in oöcytes of pupae and of adult females up to 10 hours of age. Here "the tetrads are long slender threads, fairly uniformly spaced, extending about the nucleus near the periphery." This condition was known (Metz, unpublished data) to persist through most, if not all, of the first 24 hours after emergence. Feulgen preparations of entire eggs of *Sciara ocellaris* were made from flies ranging in age from 30 to 52 hours. From 30 to 39 hours (at room temperature) the chromosomes appear as

typical, somewhat condensed late prophase tetrads. Between 40 and 42 hours the tetrads are extremely condensed on the metaphase plate. At 52 hours after the fly has emerged as an adult, the chromosomes are less condensed and appear in very late metaphase or early anaphase. Presumably they remain in this condition until fertilization takes place at the time of laying. Females of this species of *Sciara* ordinarily lay their eggs during the latter part of the second day or during the third day.

Adult females ranging in age from 23 hours to 52 hours were treated with x-rays. Owing to the fact that very high dosages had previously been used in the *Sciara* work, the first flies to be treated were given 3025 r units. This proved to be a lethal dose for oöcytes of females over 24 hours of age. Therefore, smaller dosages (1514 and 770 r units) were given later. Flies were mated immediately after treatment and in most cases a normal number of eggs was laid. Untreated virgin females of corresponding ages were also mated. From these control matings normal progenies were obtained. In all cases determinations of gross rearrangements were made on salivary gland chromosomes of the F_1 larvae. The results of these experiments are summarized in table 1.

TABLE 1

SUMMARY OF TESTS FOR X-RAY-INDUCED CHROMOSOME ABERRATIONS IN OÖCYTES OF *Sciara ocellaris*

	770 R UNITS			1514 R UNITS		
AGE OF ♀♀ X-RAYED, HRS.	NO. LARVAE EXAMINED	NO. REARRANGEMENTS	% REARRANGEMENTS	NO. LARVAE EXAMINED	NO. REARRANGEMENTS	% REARRANGEMENTS
24–26	22	0		23	0	
28–30				77	2 (1 deletion, 1 translocation)	2.6
35	10	0				
41–42	43	6 (inversions)	14	10	8 (1 deletion, 7 inversions)	80

While tests for rearrangements were being carried out, observations on the viability of zygotes from treated oöcytes were made. Eggs laid by females treated with 1514 r units were counted. The number of viable offspring was determined by totaling the number of larvae from which salivary gland smears were made and the number of flies which hatched from treated oöcytes. Since this dosage is so nearly lethal for oöcytes in or near metaphase, the percentages of viable offspring of flies treated between 36 and 49 hours of age are based on small numbers. However, the numbers of eggs laid by flies of these ages were large. There seems to be a significant reduction in viability of eggs from females treated between the ages of 30 and 36 hours. This low viability rate of 1 to 3% also obtains if treatment is given at metaphase or early anaphase. It is obvious that oöcytes increase in sensitivity as they pass through the late prophase

stage of meiosis. This relation of viability to phases of meiosis is being investigated further.

The question is raised as to whether these results can be correlated with those secured in the *Drosophila* work. The fact that all stages of oögonia and oöcytes in *Drosophila* are rayed simultaneously must be taken into consideration, whereas in *Sciara* all oöcytes in any one individual female are in the same stage of development when treated. Consequently at the most sensitive stages here a higher frequency of rearrangements would be expected, while at the more "resistant" stages a lower frequency would obtain. These data conform to that expectancy. It is interesting to note that the metaphase is the most sensitive stage and that here, even with comparatively low dosages, a high frequency of breaks occurs. It is to be concluded that there is a distinct difference between frequencies of gross chromosome aberrations obtained in treating males and females with x-radiation, but that this difference is not a matter of sex. It depends upon the condition of chromosomes of germ cells at the time of treatment. In a subsequent paper a detailed comparison will be made of the results of the present investigation with those of other investigators concerning the effect of x-rays in producing chromosome rearrangements with reference to the mitotic phases of cell division.

Metz and Boche (loc. cit.) and Metz and Bozeman (loc. cit.) have suggested that in oöcytes of *Sciara* rayed during the pupal and early adult stages the tetrads may be held in a matrix of relatively firm gel, thus being permitted limited movement, and that this may explain the failure to obtain rearrangements in these stages. It is noteworthy that in the present investigation two rearrangements were found to have occurred shortly after the tetrads had begun to exhibit the typical activity of late prophase chromosomes.

Further experiments are being designed to test the hypothesis, suggested by Metz,[11] regarding the effect of irradiation on the matrix or sheath material and its relation to activity of movement of chromosomes. It is suggested here that the effect of irradiation on the division apparatus may play a part in reducing viability of oöcytes rayed at or near metaphase. This possibility is being investigated.

One problem of current interest in connection with induced chromosome rearrangements is that of determining whether rearrangement occurs at the time of treatment or is delayed for a considerable period.[12] In the present case a known interval of time elapsed between treatment and the completion of the first meiotic division, and the theoretically expected results would depend on whether rearrangement occurred during this interval or later, that is, before or after meiosis. If rearrangement occurs before the first meiotic division is completed, the number of cases involving translocations in which a viable combination of chromosomes would pass into

the second oöcyte would be expected to be very small relative to the number of cases involving inversions. A large percentage of the former would be eliminated by the meiotic process, due to the formation of aneuploid gametes. Since Metz and Boche found an equal number of translocations and inversions after treatment of sperm, where the chromosomes had already passed through the maturation process, it would seem probable that an approximately equal number of translocations and inversions would occur (but not be recovered) in the present case. The fact that only one translocation was recovered, in contrast to 13 inversions, seems to indicate that, in this case, all the rearrangements occurred before the end of the first meiotic division.

* The author is indebted to Dr. C. W. Metz for suggesting this problem and for furnishing materials, to the University of Pennsylvania for space and facilities in the Zoölogical Laboratories and for x-ray treatments given at the Department of Radiology of the University Hospital. This investigation has been aided by a grant from the General Education Board.

[1] Metz, C. W., and Boche, R. D., these PROCEEDINGS, **25**, 280 (1939).
[2] Smith-Stocking, Helen, *Genetics*, **21**, 421 (1936).
[3] Muller, H. J., *Proc. 6 Int. Cong. Genetics*, **1**, 213 (1932).
[4] Oliver, C. P., *Zeit. f. induk. Abstam.- u. Vererb.-lehre*, **61**, 447 (1932).
[5] Shapiro, N. J., and Volkova, K. V., *Biol. Zhurn.*, **7**, 578 (1938).
[6] Glass, H. B., *Genetics*, **25**, 117 (1940).
[7] Metz, C. W., and Bozeman, Martha Lee, these PROCEEDINGS, **26**, 228 (1940).
[8] Whiting, Anna R., *Jour. Exp. Zool.*, **83**, 249 (1940).
[9] Patterson, H. B., *Genetics*, **18**, 32 (1933).
[10] Sonnenblick, B. P., these PROCEEDINGS, **26**, 373 (1940).
[11] Metz, C. W., *Ibid.*, **20**, 159 (1934).
[12] See Kaufmann, B. P., *Ibid.*, **27**, 18 (1941).

THE INFRA-RED SPECTRA OF SiH_4 AND GeH_4

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In a recent note[1] we have reported on the preliminary results on the measurement of the frequencies ν_2 and ν_4 in the infra-red spectra of GeH_4 and SiH_4 which lie in the region from 9.0μ to 14.0μ. The measurements have now been extended to embrace also the fundamental bands ν_3 in the spectra of these molecules. Inasmuch as considerable time will be required to study exhaustively the data gathered, it has seemed worth while to present a few facts concerning these spectra and a little of the information to be derived from them.

The band ν_3 in the SiH_4 spectrum is shown in figure 1. Curve 1-*A* was

obtained using an absorption cell 6 cm. long containing gas to a pressure of 12 cm. Hg. The second curve, 1-*B*, was made using the same cell, but with a gas pressure of 6 cm. Hg. The former may be said to verify with high fidelity the measurements reported by Steward and Nielsen[2] on this spectrum when one considers that the improvement effected in the resolution since that time justifies the recording of data at intervals $^1/_6$ of those used by them. The second curve contains the same details, but the relative heights of the lines are markedly different. The conclusion to be drawn from the two curves is that in the former case too much gas was present so that the stronger lines are much "overexposed," with the weaker

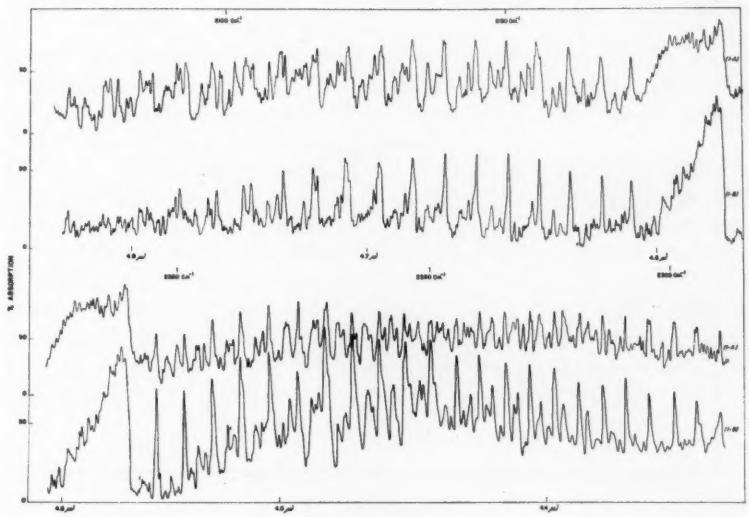

FIGURE 1

detail much overemphasized. We consider curve 1-*B* to be a much more accurate representation of the appearance of the band ν_3 in the spectrum of SiH_4 than curve 1-*A*.

These results lead directly to an interesting point concerning the band ν_3 in the spectrum of GeH_4. The original measurements reported by Steward and Nielsen[3] on this spectrum indicated that between the principal lines was to be found much weaker satellite lines. The presence of the satellite lines was verified by Lee and Sutherland,[4] but these investigators found them to be much more intense than was indicated in the work of Steward and Nielsen. We have investigated this point and we find that we can reproduce either the results of Steward and Nielsen or those ob-

tained by Lee and Sutherland depending upon how much gas is present in the absorbing layer.

Using a cell 10 cm. long filled with gas to a pressure of 5 cm. Hg the curve of Steward and Nielsen can be quite faithfully duplicated when one considers the fact that the effective resolving power of the instrument has been greatly increased since the earlier measurements were made. The results of Lee and Sutherland are best duplicated (except that ours show considerably more detail) when the same cell is filled to a pressure of 10 cm. Hg, in which case the principal lines are much "overexposed." This curve is shown in figure 2-*A*. A much more reliable representation of the actual appearance of the band ν_3 in this spectrum, we believe, is depicted in figure 2-*B* which was obtained using the above cell with only about 1

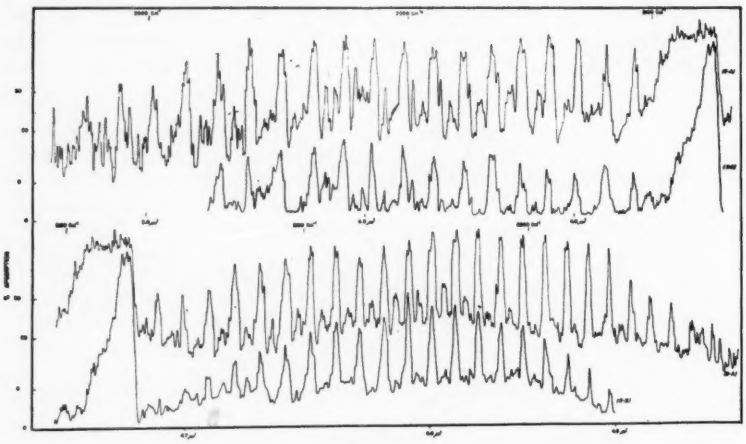

FIGURE 2

cm. Hg pressure. In this curve the satellites are quite faint and certainly cannot be regarded as of first order of magnitude. The only disturbing point is that the measurements of Lee and Sutherland and those by Steward and Nielsen were apparently carried out with the same equivalent absorbing layer and should therefore look alike. It should be pointed out that in the earlier experiment made by Steward and Nielsen there was evidence that some free hydrogen was present in the GeH_4 gas so that the pressure read on the manometer may have been due in part to the presence of this hydrogen. No attempt was made at that time to remove any hydrogen which was present since this gas would have no infra-red spectrum.

The three fundamentals ν_2, ν_3 and ν_4 studied in the spectra of these two molecules have been sufficiently well resolved so that the moments of inertia

of the molecules may be determined. In the first six columns of table 1 the frequency positions of the bands ν_2, ν_3 and ν_4 and the average spacings between two rotation lines $\Delta\nu_i$ in the three bands are given for the two molecules.

A molecule of the tetrahedral XY_4 type is in zeroth approximation a spherical top with only a single principal moment of inertia so that one might expect all of the bands to have the same average spacing between two adjacent rotation lines. This is not the case, however, because the frequencies ν_3 and ν_4 which are threefold degenerate have an internal angular momentum of oscillation associated with them so that Coriolis interactions are set up between the rotational motion and the oscillatory motion of the molecule when it is vibrating in one of these modes. It has been pointed out by Teller[5] that the moment of inertia I cannot *in such cases* be determined from the usual formula $\Delta\nu = h/4\pi^2cI$, but rather by the relation $\Delta\nu_3 + \Delta\nu_4 = 3h/8\pi^2cI$. The values of the moments of inertia I for the two molecules determined in this manner are given in the seventh column of table 1.

The forbidden frequency ν_2, which is twofold degenerate, becomes optically active because of a resonance Coriolis interaction between it and the frequency ν_4. The amplitude of the internal angular momentum associated with ν_2 itself is zero so that the Coriolis interaction between the rotational motion and the oscillatory motion of the molecule vanishes when it oscillates in this mode. This gives an independent method of determining the moments of inertia since here the relation $\Delta\nu_2 = h/4\pi^2cI$ is again valid. The values of I obtained in this manner are given in the eighth column of table 1.

TABLE 1

INFORMATION CONCERNING THE SPECTRA AND STRUCTURE OF SiH_4 AND GeH_4

	ν_3 CM.$^{-1}$	$\Delta\nu_3$ CM.$^{-1}$	ν_2 CM.$^{-1}$	$\Delta\nu_2$ CM.$^{-1}$	ν_4 CM.$^{-1}$	$\Delta\nu_4$ CM.$^{-1}$	$I(\nu_2\nu_4)$ G.-CM.^{2}	$I(\nu_2)$ G.-CM.^{2}	X–H DISTANCE CM.
SiH_4	975	5.62	2191	5.64	910	2.77	0.998×10^{-39}	0.996×10^{-39}	1.50×10^{-8}
GeH_4	932	5.275	2114	5.67	818	2.27	1.057×10^{-39}	1.061×10^{-39}	1.54×10^{-8}

From the average values of I obtained in the above manner we have determined the Si–H distance and the Ge–H distance and these are set down in the ninth column of table 1.

In making these calculations we have neglected entirely the satellite structure in these bands. The explanation for this structure is not entirely clear. In the case of the bands ν_2 and ν_4, the curves of which are not shown here, much of the complex structure is certainly due to the Coriolis-resonance interaction which exists between the two vibrations. Some of the structure in ν_4 is undoubtedly due to the presence of the isotopic molecules. In the case of the band ν_3 in the spectrum of SiH_4 it seems possible

to account for most of the satellites on the basis of three isotopes of Si. In the case of the band ν_3 in the spectrum of GeH_4 it does not seem possible to account for the secondary structure wholly on this basis. On the other hand, the secondary structure is in reality faint and can probably be attributed to several causes. For example, they may be a faint overtone band, say $3\nu_4$, lying in this region or they may be due to the splitting of the principal lines into components caused by centrifugal distortion of the molecule. Until a more intensive study of the data has been made on the basis of the theory of such molecules it seems necessary to postpone this question.

It is surprising to note that the two molecules have almost the same radius which is nearly $\sqrt{2}$ times that of the methane molecule. It is felt, however, that the data are so definite that little doubt can remain concerning the values $\Delta\nu_2$, $\Delta\nu_3$ and $\Delta\nu_4$ from which the moments of inertia and the X–H distances have been computed.

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[1] Straley, J. W., Tindal, C. H., and Nielsen, H. H., *Phys. Rev.*, **58**, 1002 (1940).
[2] Steward, W. B., and Nielsen, H. H., *Phys. Rev.*, **47**, 828 (1935).
[3] Steward, W. B., and Nielsen, H. H., *Ibid.*, **48**, 861 (1935).
[4] Lee, E., and Sutherland, G. B. B. M., *Cambridge Phil. Soc., Proc.*, **35**, 341 (1939).
[5] Teller, E., *Hand- und Jahrbuch Chem. Phys.*, **9**, II, 43 (1934).

MAXIMAL SUBGROUPS OF A FINITE GROUP

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It is possible to construct a cyclic group which contains exactly an arbitrary given number $k > 1$ of maximal proper subgroups. To do this it is only necessary to form the direct product of k cyclic groups of distinct prime power orders. Each of these k groups is known to contain one and only one maximal proper subgroup whenever the order of such a group is not a prime number. The ϕ-subgroup of such a group G is composed of all of its operators whose orders are not divisible by the highest power of at least one prime number which divides the order of the group. The ϕ-quotient group has for its order the product of all the distinct prime numbers which divide the order of G and the k maximal subgroups of G correspond to the subgroups of prime index in this quotient group. When $k = 1$ and the order of G is a prime number then G contains no maximal proper subgroup but when the order of G is a larger power of a prime

number and $k = 1$ it obviously contains one and only one maximal proper subgroup.

When a group G contains one and only one maximal proper subgroup it is therefore the cyclic prime power group of composite order and when it contains two and only two maximal proper subgroups it is obviously cyclic, since these two subgroups are invariant and the operators of G which do not appear in at least one of them must include generators of G. Therefore they could not all appear in the other maximal subgroup and an operator which is not contained in at least one maximal proper subgroup must generate the group. Hence it results that when a group contains two and only two maximal proper subgroups it is the cyclic group which is the direct product of two cyclic groups of distinct prime power orders as was noted in these PROCEEDINGS, **27,** 69 (1941), as a result of a somewhat different argument. It therefore results that whenever a group has either exactly one or exactly two maximal proper subgroups it belongs to the system of groups noted in the preceding paragraph.

Whenever a maximal subgroup of G is invariant under another maximal subgroup of G it is invariant under G since these two maximal subgroups of G generate G. In particular, the permutation group according to which the non-invariant maximal proper subgroups of G are transformed under G cannot have a transitive constituent of degree two since the maximal subgroups corresponding to the two letters of such a constituent would transform each other into themselves and hence these letters would correspond to invariant subgroups of G, which is a contradiction. The permutation group according to which all the maximal proper subgroups of G are transformed under G could not be transitive since a transitive permutation group of degree n contains at least $n - 1$ permutations which involve all the letters of the permutation group. If G contains non-invariant maximal subgroups they must be transformed under G according to a permutation group each of whose transitive constituents is at least of degree 3 whenever the constituent is not the identity.

From the preceding paragraph it results that if G contains exactly three maximal proper subgroups they are invariant under G. If the invariant cross-cut of two of them does not appear in the third of these invariant subgroups then G must be cyclic because not all of the operators of G which do not appear in the first two of the three invariant maximal proper subgroups could appear in the third of these subgroups since these operators generate the cross-cut of the first two of them. If an abelian group contains three and only three maximal proper subgroups its order cannot be divisible by more than three distinct prime numbers since each of its maximal subgroups contains all of its Sylow subgroups save one. When the three maximal subgroups are supposed to have no common cross-cut the order of the group is not the power of a single prime number. It

therefore results that if a group contains exactly three maximal proper subgroups which do not have a common cross-cut then it is the direct product of three cyclic prime power groups whose orders are relatively prime.

When the three maximal proper subgroups of G have a common cross-cut the corresponding quotient group involves operators of prime order since the quotient group of G with respect to a maximal invariant subgroup is of prime order. The order of the former quotient group is therefore p^2, and since G is assumed to contain exactly three maximal subgroups this quotient group must be the four group. All the operators of G appear in its three maximal proper subgroups since G cannot be cyclic. As a cyclic group whose order is not a power of a single prime number is the direct product of its cyclic Sylow subgroups it results from the first paragraph of this article that *the number of the maximal proper subgroups of any cyclic group of composite order is equal to the number of the distinct prime numbers which divide the order of the group.* Hence there results the following theorem: *If in a group which has exactly three maximal subgroups these subgroups have a common cross-cut then this group is of order* 2^m *and has two independent generators, and vice versa.*

If a group G contains exactly k maximal proper subgroups then the direct product of G and a group which contains exactly l maximal proper subgroups and whose order is prime to the order of G contains exactly $k + l$ maximal proper subgroups. In particular, since every abelian group is the direct product of its Sylow subgroups it results that the exact number of the maximal proper subgroups of an abelian group is the sum of the exact numbers of the maximal proper subgroups of its Sylow subgroups. The exact number of the maximal proper subgroups of a Sylow group is equal to the number of its subgroups of prime index and hence it is equal to the number of its subgroups of order p in its ϕ-quotient group. The determination of the exact number of the maximal proper subgroups of any abelian group is therefore reduced to the addition of the numbers of its subgroups of prime order in the ϕ-quotient groups of its Sylow subgroups.

It was noted above that the number of the maximal proper subgroups of any given cyclic group is equal to the number of the distinct prime numbers which divide the order of this cyclic group. It may also be noted here that whenever the number of the maximal proper subgroups of an abelian group is equal to the number of its Sylow subgroups then the group must be cyclic and hence it is the direct product of its Sylow subgroups. In particular, if an abelian group contains exactly four maximal proper subgroups and is non-cyclic it contains at most two Sylow subgroups since a non-cyclic Sylow group contains at least three maximal proper subgroups. That is, a non-cyclic abelian group which involves exactly four maximal proper subgroups and is not a prime power group is

the direct product of an abelian group of order 2^m which has two independent generators and a cyclic group of odd prime power order. If a prime power group contains exactly four maximal proper subgroups it is of order 3^m and contains two independent generators.

It was noted above that the total number of the maximal proper subgroups of G could not constitute a single set of conjugate subgroups under G since they could not be transformed under G according to a transitive permutation group. The transitive permutation group according to which a set of conjugate maximal proper subgroups is transformed under G must be primitive since its subgroup composed of all its permutations which omit one letter is maximal. Every invariant subgroup of such a group is therefore transitive and if G contains one and only one set of conjugate maximal proper subgroups it must involve at least one invariant maximal proper subgroup. A maximal invariant proper subgroup is evidently of prime index under the group but a maximal non-invariant proper subgroup is not always of prime index as results from the tetrahedral group.

If G has exactly four maximal proper subgroups they are either all invariant under G or one of them is invariant and the other three are conjugate. In the latter case these three conjugate subgroups are transformed under G according to the symmetric group of degree 3 since they could not be transformed according to the cyclic group of this degree. Hence G is then isomorphic with the non-cyclic group of order 6 and its four maximal proper subgroups correspond to the maximal proper subgroups of this non-cyclic group. To every maximal proper subgroup of a quotient group of a given group there evidently corresponds a maximal proper subgroup of the group. In the present case G could not contain a maximal proper subgroup which would involve operators corresponding both to operators of order 2 and to operators of order 3 in the given quotient group.

The Sylow subgroups of G whose orders are powers of 3 are conjugate under the invariant subgroup of G which corresponds to the subgroup of order 3 in the given quotient group. Hence each of these Sylow subgroups is transformed into itself by operators which correspond to operators of order 2 in the given quotient group. At least one of the operators has an order which is a power of 2. If this operator and the given Sylow subgroup would not generate G there would be more than four maximal proper subgroups in G. Hence there results the following theorem: *If a group contains exactly four maximal proper subgroups such that one of them is invariant and the other three are conjugate under G then G involves an invariant subgroup whose order is a power of* 3 *and G may be obtained by extending this subgroup by an operator whose order is a power of* 2 *and transforms this subgroup into itself.*

When every maximal subgroup of G is invariant every such subgroup

gives rise to a quotient group of prime order as was noted above. If two such subgroups give rise to quotient groups of the same prime order p their cross-cut gives rise to the non-cyclic group of order p^2, and if two such subgroups give rise to quotient groups of different prime orders their cross-cut gives rise to the cyclic group whose order is the product of these two prime numbers. From these facts it follows directly that if all the maximal proper subgroups of G are invariant then G is the direct product of its Sylow subgroups and vice versa. Cf. O. Ore, *Duke Mathematical Journal*, **5**, 431 (1939).

ON FUNCTIONS WHOSE DERIVATIVES DO NOT VANISH IN A GIVEN INTERVAL

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In what follows, J denotes an interval on the real axis and $f(x)$ denotes a function taking real values and possessing all derivatives in J. D. V. Widder proved recently[1] the following interesting theorem.

W. If, for $m = 0, 1, 2, \ldots,$

$$(-1)^m f^{(2m)}(x) \geqq 0$$

in J, then $f(x)$ *is an entire function of exponential type.*[2]

Theorem W is closely related to the following result of Serge Bernstein.[3]

B. If no derivative of $f(x)$ *changes sign in J and if there exists a fixed k, such that it is impossible to find more than k successive derivatives of* $f(x)$ *whose absolute values vary all in the same direction (all increase or all decrease), then* $f(x)$ *is an entire function of exponential type.*

Theorem B is of a more general character than theorem W but B does not contain W because B assumes and W does not assume that each derivative of odd order has a constant sign in J. To the problem arising from this situation I should like to contribute the following theorems.

I. *Let* α *be a real number,* $0 < \alpha < \pi$. *If*

$$f^{(n)}(x) \sin (n + 1)\alpha \geqq 0$$

in J for $n = 0, 1, 2, 3, \ldots,$ *then* $f(x)$ *is an entire function of exponential type.*

II. *If, for* $m = 0, 1, 2, \ldots,$

$$f^{(4m)}(x) \geqq 0$$

in J and $f^{(4m+1)}(x)$ reaches its maximum in J in the left-hand end-point of J, then $f(x)$ is an entire function of exponential type.

Theorem I contains W as the special case $\alpha = \pi/2$. II contains W because, if $f^{(4m+2)}(x) \leqq 0$ in J, $f^{(4m+1)}(x)$ reaches certainly its maximum in J in the left-hand end-point. But II is evidently not contained in B. Concerning I, we have to distinguish two cases. If α is a rational multiple of π, $\sin(n+1)\alpha$ vanishes for an infinity of integers n, and the theorem I makes no hypothesis on the sign of the corresponding $f^{(n)}(x)$ and so this case is not contained in B. If α is not a rational multiple of π, each derivative of $f(x)$ is supposed to keep a constant sign in J, and this case of I is, as a little consideration shows, contained in B.

Outline of the Proofs.—Admit that J is the interval $0 \leqq x \leqq 1$. For both theorems, I and II, I use the formula of partial integration written as follows.

$$\int_0^a S^{(n)}(a-t)F(t)dt = \int_0^a S(a-t)F^{(n)}(t)dt + \sum_{\nu=0}^{n-1}\left(S^{(n-\nu-1)}(a)F^{(\nu)}(0) - S^{(n-\nu-1)}(0)F^{(\nu)}(a)\right) \quad (1)$$

I. Put in (1)

$$a = \pi, \quad S(t) = e^{t \operatorname{cotg} \alpha} \sin t, \quad F(t) = f(xt/\pi).$$

We can find arbitrarily large integers n such that

$$\frac{n\alpha}{\pi} - \left[\frac{n\alpha}{\pi}\right] < 1 - \frac{\alpha}{\pi},$$

$$\frac{n\alpha}{\pi} - \left[\frac{n\alpha}{\pi}\right] \leqq \frac{(\nu+1)\alpha}{\pi} - \left[\frac{(\nu+1)\alpha}{\pi}\right] \text{ for } \nu = 0, 1, 2, \ldots, n-2.$$

Owing to this choice of n, by the hypothesis of theorem I, all terms on the right hand side of (1) become of the same sign and we obtain an appropriate estimate for the derivatives of $f(x)$.

II. There exists a positive characteristic value a such that the differential equation $y'''' = y$ possesses an integral $y = S(x)$ satisfying the following conditions:

$$S(0) = S'(0) = S(a) = S'(a) = 0,$$

$$S(x) > 0 \text{ for } 0 < x < a.$$

Put this $S(x)$, this a, $n = 4m (m = 1, 2, 3, \ldots)$ and $F(t) = f(xt/a)$ in (1) and an appropriate estimate for the derivatives of $f(x)$ readily follows.

[1] *Proc. Nat. Acad. Sci.*, **26**, 657–659 (1940). A simpler proof was communicated to the New York meeting of the American Mathematical Society, February 22, 1941, by R. P. Boas. Essentially the same proof was found independently by I. J. Schoen-

berg. The idea of this proof is used in the following. I am indebted to Mr. Boas for information about the literature of the subject.

[2] I.e., there exists a positive constant a such that $f(z)e^{-a|z|}$ is bounded for all values of z.

[3] *Comm. Kharkov Math. Soc.*, Series 4, **2**, 1–11 (1928). (See p. 5.)

NOTE ON A CANONICAL FORM FOR THE LINEAR q-DIFFERENCE SYSTEM

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The modern theory of ordinary linear q-difference equations may be considered definitely to have evolved with the appearance of papers by R. D. Carmichael[1] and G. D. Birkhoff[2] announcing what was then regarded as a general theory. Proof of the existence of a full complement of formal solutions in the truly general case and an investigation of their convergence was later given by C. R. Adams.[3] More recently W. J. Trjitzinsky[4] has discovered a full complement of analytic solutions and has developed certain of their asymptotic properties.

As a point of departure either the single linear q-difference equation of the nth order or the equivalent q-difference system may be employed. It is the purpose of this note to announce the existence and indicate the derivation of a canonical form for the linear q-difference system of the nth order analogous to that found by Birkhoff for the linear differential system.[5] Consider the matrix form of the q-difference system

$$Y(qx) = A(x)Y(x), \qquad |q| \neq 1, \tag{1}$$

where $A(x)$ is analytic or has a pole at $x = \infty$, and $|A(x)| \not\equiv 0$. From the work of Adams cited above, such a system (1) has always a full complement of n formal solutions, which in the typical case that certain rational numbers $\mu_1, \mu_2, \ldots, \mu_n$ are all distinct may be written (after a simple preliminary transformation) in the form

$$Y(x) = (s_{ij}(x))(q^{\frac{\mu}{2}(i^2-i)}x^{\mu i}\delta_{ij}),$$

where the $s_{ij}(x)$ are power series of the form $\sum_{k=0}^{\infty} s_{ijk}x^{-k}$, $(s_{ij}(\infty)) = (\delta_{ij})$. In this case the matrix $A(x)$ in (1) has the special form

$$(x^{\mu_i} q^{r_i} a_{ij}(x)),$$

where the $a_{ij}(x) - \delta_{ij}$ vanish to arbitrarily high order at $x = \infty$. Without loss of generality it may be assumed that the μ_i are all integers and such that $\mu_1 > \mu_2 > \ldots > \mu_n \geqq 0$, and that $|q| > 1$.

To the system (1) is related an adjoint system

$$Z(qx) = Z(x)A^{-1}(x) \tag{2}$$

which has formal solutions

$$Z(x) = (z_{ij}(x)) = (q^{-\frac{\mu_i}{2}(i^2-i)} x^{-r_i\delta_{ij}})(t_{ij}(x)),$$

where the $t_{ij}(x)$ are series in descending powers of x, and the kth of the n basic sets of solutions consists of the elements $z_{k1}, \ldots, z_{kn}$. But from the above-mentioned work of Adams it follows that the formal solutions corresponding to the least value of μ_i, i.e., $-\mu_1$, are actual solutions as well. Thus the elements $z_{11}(x), \ldots, z_{1n}(x)$ constitute an analytic solution of (2) in the neighborhood of $x = \infty$. Then for $\cdot Z(x) = (z_{1j})$ (a matrix having all rows alike) it follows that

$$\cdot Z(qx)\,Y(qx) = \cdot Z(x)A^{-1}(x)A(x)\,Y(x) = \cdot Z(x)\,Y(x)$$

so that

$$\sum_{j=1}^{n} z_{1j}(qx)y_j(qx) = \sum_{j=1}^{n} z_{1j}(x)y_j(x) = p(x),$$

where $p(x)$ is a q-periodic function. The change of variable

$$\begin{aligned} \bar{y}_1 &= \sum_{j=1}^{n} t_{1j}(x)y_j(x) = q^{\frac{\mu_1}{2}(i^2-i)} x^{r_1} \sum_{j=1}^{\infty} z_{1j}\, y_j \\ \bar{y}_j &= y_j, \qquad j = 2, \ldots, n \end{aligned} \tag{3}$$

then transforms the system (1) into a system (dropping the bars on the y's and a's)

$$\begin{aligned} y_1(qx) &= x^{\mu_1} q^{r_1} y_1(x) \\ y_2(qx) &= a_{21}(x)y_1(x) + \ldots + a_{2n}y_n(x) \\ &\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots \\ y_n(qx) &= a_{n1}(x)y_1(x) + \ldots + a_{nn}y_n(x). \end{aligned} \tag{4}$$

This new system has n independent sets of formal solutions with μ_i's and r_i's distributed as in the original system. Furthermore the matrix $(a_{ij}(x))$, $i, j = 2, \ldots, n$ is rational at $x = \infty$ and of determinant not identically

zero. The corresponding matrix of independent formal solutions is obtained from that of (4) by deleting the first row and column.

In the case $n = 2$ the system (4) becomes (with μ's and r's in inverted order)

$$\begin{aligned} y_1(qx) &= x^{\mu_2}q^{r_2}y_1(x) \\ y_2(qx) &= a_{21}(x)y_1(x) + a_{22}(x)y_2(x). \end{aligned} \tag{5}$$

Let $y_2(x) = q^{\frac{\mu_1}{2}(i^2-i)}x^{r_1}s(x)$ in the solution for which $y_1 \equiv 0$. Then the change of variable $y_1 = \bar{y}_1$, $y_2 = s(x)\bar{y}_2$ converts (5) into

$$\begin{aligned} y_1(qx) &= x^{\mu_2}q^{r_2}y_1(x) \\ y_2(qx) &= a_{21}(x)y_1(x) + x^{\mu_1}q^{r_1}y_2(x). \end{aligned} \tag{6}$$

Now by means of a transformation $\bar{y}_1 = y_1$, $\bar{y}_2 = \alpha(x)y_1 + y_2$, where $\alpha(x) = \sum_{i=0}^{\infty} c_i x^{-i}$ is to be determined, it is found that the corresponding coefficient in the transformed system is

$$\bar{a}_{21}(x) = \alpha(qx)x^{\mu_2}q^{r_2} - \alpha(x)x^{\mu_1}q^{r_1} + a_{21}(x). \tag{7}$$

This implies the following relationship between coefficients of ith powers of x:

$$\bar{a}_{21i} = \frac{c_{i+\mu_2}q^{r_2}}{q^{i+\mu_2}} - c_{i+\mu_1}q^{r_1} + a_{21i}. \tag{8}$$

For convenience let $\bar{a}_{21i} = \bar{a}_i$, $a_{21i} = a_i$, $\mu_2 - \mu_1 = p$, and replace $i + \mu_2$ by i. Then (8) becomes

$$\bar{a}_{i-\mu_2} = \frac{c_i q^{r_2}}{q^i} - c_{i-p}\,q^{r_1} + a_{i-\mu_2}. \tag{9}$$

For simplicity in this report consider in detail only the case $p = 1$. Take i_0 arbitrarily large and set $c_{i_0} = 0$. Then $\bar{a}_{i_0-\mu_2}$ can be made zero by choosing $c_{i_0-1} = q^{-r_1}a_{i_0-\mu_2}$ as dictated by (9). This process can be repeated until c_0 is determined. There remains only the relation $\bar{a}_{-\mu_2} = c_0 q^{r_2}$ to be satisfied, which is taken as the definition of $\bar{a}_{-\mu_2}$. The coefficients $c_{i_0-2}, \ldots, c_0$ thus determined are given by the formula

$$c_i = q^{-r_2}a_{i+1-\mu_2} + \sum_{j=2}^{i_0-i} a_{i+j-\mu_2}q^{\frac{-j(j-1)}{2} + (j-1)(r_2-i) - jr_1} \tag{10}$$

for $i = 0, \ldots, i_0 - 2$. Now let $i_0 \longrightarrow \infty$. The series in (10) plainly is convergent for every $i \geqslant 0$. Thus $c_0, c_1, c_2, \ldots$ are so determined that by the transformation $\bar{y}_1 = y_1$, $\bar{y}_2 = \alpha(x)y_1 + y_2$, $\bar{a}_{21}(x)$ may be reduced, in the case $p = 1$, to the simple form

$$\bar{a}_{21}(x) = c_0 q^{r_2} x^{\mu_2}.$$

For the more detailed but equally straightforward case where $p > 1$ the resulting form is

$$\bar{a}_{21}(x) = x^{\mu_2} q^{r_2} \sum_{i=0}^{p-1} c_i (qx)^{-i}.$$

The system (1) of the second order may consequently be transformed into the canonical system

$$\begin{aligned} y_1(qx) &= x^{\mu_2} q^{r_2} y_1(x) \\ y_2(qx) &= x^{\mu_2} q^{r_2} \Big(\sum_{i=0}^{p-1} c_i (qx)^{-i} \Big) y_1(x) + x^{\mu_1} q^{r_1} y_2(x). \end{aligned} \tag{11}$$

A canonical form for the system of order three is obtained by first applying the corresponding transformation (3). The solutions of the resulting system of form (4) for which $y_1 \equiv 0$ satisfy a second order system in y_2, y_3 which may be treated as outlined above for the general second order system. Then by means of a first transformation of the form $\bar{y}_1 = y_1$, $\bar{y}_2 = \beta(x) y_1 + y_2$, $\bar{y}_3 = y_3$ where $\beta(x)$ is determined by the method resulting from (9) the coefficient $a_{21}(x)$ may be reduced to $x^{\mu_3} q^{r_3} \big(\sum_{i=1}^{\bar{p}-1} i (qx)^{-i} \big)$, where $\bar{p} = \mu_3 - \mu_2$. Also by a transformation $\bar{y}_1 = y_1$, $\bar{y}_2 = y_2$, $\bar{y}_3 = \gamma(x) y_1 + y_3$, $a_{31}(x)$ may be similarly reduced. Continuing in this manner by an induction on the order of the system there is obtained in all cases a canonical form for the system of order n striking in its simplicity and symmetry. For (1) of order n, the equivalent system may be written in the form

$$\begin{aligned} y_1(qx) &= x^{\mu_n} q^{r_n} y_1(x) \\ y_2(qx) &= x^{\mu_n} q^{r_n} c_{21}(x) y_1(x) + x^{\mu_{n-1}} q^{r_{n-1}} y_2(x) \\ &\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots \\ y_n(qx) &= x^{\mu_n} q^{r_n} c_{n_1}(x) y_1(x) + \ldots + x^{\mu_2} q^{r_2} c_{n,n-1}(x) y_{n-1}(x) + x^{\mu_1} q^{r_1} y_n(x) \end{aligned} \tag{12}$$

where the $c_{ij}(x)$ are polynomials in $1/x$ of the form $c_{ij}(x) = \sum_{k=0}^{\alpha_{ij}} c_{ijk} (qx)^{-k}$ and $\alpha_{ij} = \mu_{n+1-j} - \mu_{n+1-i} - 1$. A detailed treatment of all cases will be found in Guenther's doctoral dissertation, and this together with further developments in a joint paper which the authors expect to offer to *Acta Mathematica*.

Up to the present time the theory of linear q-difference equations has lagged noticeably behind the sister theories of linear difference and differential equations. In the opinion of the authors the use of the canonical system, as formulated above in a special case, is destined to carry the

theory of q-difference equations to a comparable degree of completeness. This program includes in particular the complete theory of the convergence and divergence of formal series, the explicit determination of the essential transcendental invariants (constants in the canonical form), the inverse Riemann theory both for the neighborhood of $x = \infty$ and in the complete plane (case of rational coefficients), explicit integral representation of the solutions, and finally the definition of q-sigma periodic matrices, so far defined essentially only in the case $n = 1$. Because of its extensiveness this material cannot be presented here.

[1] Carmichael, R. D., "The General Theory of Linear q-Difference Equations," *Am. Jour. Math.*, **34**, 147–168 (1912).

[2] Birkhoff, G. D., "The Generalized Riemann Problem...," *Proc. Am. Acad.*, **49**, 521–568 (1913).

[3] Adams, C. R., "On the Linear Ordinary q-Difference Equation," *Ann. Math.*, Ser. II, **30**, No. 2, 195–205 (1929).

[4] Trjitzinsky, W. J., "Analytic Theory of Linear q-Difference Equations," *Acta Mathematica*, **61**, 1–38 (1933).

[5] Birkhoff, G. D., "Singular Points of Ordinary Linear Differential Equations," *Trans. Am. Math. Soc.*, **10**, 436–470 (1909).

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*ON THE STABILITY OF THE LINEAR FUNCTIONAL EQUATION**

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The solutions of the linear functional equation $f(x + y) = f(x) + f(y)$ have been investigated for many spaces. Throughout this paper any solution $f(x)$ of this equation will be called a linear function or transformation. In a recent talk before the Mathematics Club of the University of Wisconsin, Dr. S. Ulam proposed the following problem of the "stability" of this equation. Suppose $f(x)$ satisfies this equation only approximately. Then does there exist a linear function which $f(x)$ approximates? To make the statement of the problem precise, let E and E' be Banach spaces and let δ be a positive number. A transformation $f(x)$ of E into E' will be called δ-linear if $\|f(x + y) - f(x) - f(y)\| < \delta$ for all x and y in E. Then the problem may be stated as follows. Does there exist for each $\epsilon > 0$ a $\delta > 0$ such that, to each δ-linear transformation $f(x)$ of E into E' there corresponds a linear transformation $l(x)$ of E into E' satisfying the inequality $\|f(x) - l(x)\| \leqq \epsilon$ for all x in E? This paper answers this question in the affirmative, and it is shown that δ may be taken equal to ϵ. This is clearly a best result, since the transformation $f(x) =$

$L(x) + c$, where $L(x)$ is linear and $\|c\| < \epsilon$, is evidently an ϵ-linear transformation for which $l(x) = L(x)$.

THEOREM 1. *Let E and E' be Banach spaces and let $f(x)$ be a δ-linear transformation of E into E'. Then the limit $l(x) = \lim_{n \to \infty} f(2^n x)/2^n$ exists for each x in E, $l(x)$ is a linear transformation, and the inequality $\|f(x) - l(x)\| \leqq \delta$ is true for all x in E. Moreover $l(x)$ is the only linear transformation satisfying this inequality.*

Proof. For any x in E the inequality $\|f(2x) - 2f(x)\| < \delta$ is obvious from the definition of δ-linear transformations. On replacing x by $x/2$ in this inequality and dividing by 2 we see that $\|(1/2)f(x) - f(x/2)\| < \delta/2$ for all x in E. Make the induction assumption

$$\|2^{-n}f(x) - f(2^{-n}x)\| < \delta(1 - 2^{-n}). \tag{1}$$

On the basis of the last two inequalities we find that

$$\|2^{-1}f(2^{-n}x) - f(2^{-n-1}x)\| < \delta/2$$

and

$$\|2^{-n-1}f(x) - 2^{-1}f(2^{-n}x)\| < \delta(1/2 - 2^{-n-1}).$$

Hence

$$\|2^{-n-1}f(x) - f(2^{-n-1}x)\| < \delta(1 - 2^{-n-1}).$$

Therefore, since the induction assumption (1) is known to be true for $n = 1$, it is true for all positive integers n and all x in E.

Put $q_n(x) = f(2^n x)/2^n$, where n is a positive integer and x is in E. Then

$$q_m(x) - q_n(x) = \frac{f(2^m x)}{2^m} - \frac{f(2^n x)}{2^n}$$

$$= \frac{f(2^{m-n} \cdot 2^n x) - 2^{m-n} f(2^n x)}{2^m}.$$

Therefore, if $m < n$ we can apply inequality (1) and write $\|q_m(x) - q_n(x)\| < \delta(1 - 2^{m-n})/2^m$, for all x in E. Hence $\{q_n(x)\}$ is a Cauchy sequence for each x in E, and since E is complete, there exists a limit function $l(x) = \lim_{n \to \infty} q_n(x)$. Let x and y be any two points of E. Since $f(x)$ is δ-linear, $\|f(2^n x + 2^n y) - f(2^n x) - f(2^n y)\| < \delta$ for all positive integers n. On dividing by 2^n and letting n approach infinity we see that $l(x + y) = l(x) + l(y)$. If we replace x by $2^n x$ in the inequality (1), we find that $\|f(2^n x)/2^n - f(x)\| < \delta(1 - 2^{-n})$. Hence in the limit, $\|l(x) - f(x)\| \leqq \delta$.

Suppose that there was another linear transformation $L(x)$ satisfying the inequality $\|L(x) - f(x)\| \leqq \delta$ for all x in E, and such that $l(y) \neq L(y)$ for some point y of E. For any integer $n > 2\delta/\|l(y) - L(y)\|$ it is obvious that $\|l(ny) - L(ny)\| > 2\delta$, which contradicts the inequalities

$\| L(ny) - f(ny) \| \leqq \delta$ and $\| l(ny) - f(ny) \| \leqq \delta$. Hence $l(x)$ is the unique linear solution of the inequality $\| f(x) - l(x) \| \leqq \delta$.

We have established Theorem 1 without continuity restrictions. Next we shall investigate the character of the linear transformation $l(x)$ when continuity restrictions are placed on the transformation $f(x)$.

THEOREM 2. *If under the hypotheses of theorem* 1 *we suppose that* $f(x)$ *is continuous at a single point* y *of* E, *then* $l(x)$ *is continuous everywhere in* E.

Proof. Assume, contrary to the theorem, that the linear transformation $l(x)$ is not continuous. Then there exists an integer k and a sequence of points x_n of E converging to zero such that $\| l(x_n) \| > 1/k$ for all positive integers n. Let m be an integer greater than $3k\delta$. Then $\| l(mx_n + y) - l(y) \| = \| l(mx_n) \| > 3\delta$. On the other hand,

$$\| l(mx_n + y) - l(y) \| \leqq \| l(mx_n + y) - f(mx_n + y) \| + \| f(mx_n + y) - f(y) \| + \| f(y) - l(y) \| < 3\delta$$

for sufficiently large n, since $\lim_{n \to \infty} f(mx_n + y) = f(y)$. This contradiction establishes the theorem.

COROLLARY. *If under the hypotheses of Theorem* 1 *we suppose that for each* x *in* E *the function* $f(tx)$ *is a continuous function of the real variable* t *for* $-\infty < t < +\infty$, *then* $l(x)$ *is homogeneous of degree one.*

Proof. For fixed x, $f(tx)$ is a continuous δ-linear transformation of the real axis into E'. By Theorems 1 and 2, $l(tx)$ is continuous in t and hence, being linear, $l(x)$ is homogeneous of degree one.

As Ulam has pointed out, there are many interesting generalizations of the problem to be investigated. For example, one might consider an analogous problem for transformations of a topological group which satisfy the equation for homomorphisms only approximately.

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